Ecological impacts of invasive mussels (*Mytilus galloprovincialis*) colonising the canopy of kelp forests in False Bay, South Africa

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Cover photograph: Craig Foster

Abstract

Kelp forests are amongst the most productive, diverse and dynamic ecosystems on earth and kelp are ecosystem engineers, which provide a structurally-complex habitat for many marine plants and animals. The Mediterranean mussel (*Mytilus galloprovincialis*) is an aggressive invader that has been in South Africa since the late 1970s, and does not normally occur in the subtidal zone, however in 2016 this mussel was first observed growing on the heads and stipes of kelp plants (*Ecklonia maxima*) in False Bay, South Africa. The overall aim of this project was to gain a better understanding of the ecological impacts of the invasive mussel colonising the canopy of kelp forests in False Bay. It was found that *M. galloprovincialis* were more likely to occur on the outer edge of kelp beds, where there is more water movement, and mussel masses are much more frequently found on kelp heads than on stipes. In addition, mussels infecting the kelp beds were likely younger than three years, indicating that colonisation has been a recent event. While the buoyancy of kelp plants was reduced by the invasion of mussels, it was not enough to sink most kelp plants. The mussel masses created habitat that increased species richness on both infected heads and stipes, and six species that are alien to the Western Cape were identified on the infected kelp plants. As detached kelps can raft vast distances, there is thus potential to spread not only alien species, but also native South African species to locations where they could become invasive. Lastly, a new species of amphipod that burrows into the primary blades of kelp heads was discovered during the course of the study. Further investigation is required to determine if the infection rate of kelp forests in False Bay is increasing and whether this phenomenon occurs in other locations.

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Introduction and literature review

Importance of kelp forests

Kelp forests are amongst the most productive, diverse and dynamic ecosystems on earth (Mann 1973). They are more varied and prolific than terrestrial forests, despite achieving smaller heights and having a much shorter lifespan (Steneck et al. 2002). Kelp forests are found throughout the temperate and polar regions in both hemispheres, their distribution being constrained by light intensity, temperature and nutrient availability (Steneck et al. 2002). When sea temperatures are too high and nutrient levels are low the kelp can become physiologically stressed and die (Gerard 1997; Tegner et al. 1996). Although kelp forests are sensitive to disturbance, they play an important role in creating new habitats (Mann 1973).

Kelp plants are ecosystem engineers, since they provide a structurally-complex habitat for many marine plants and animals, such as mammals, crustaceans, fish, algae, echinoderms and molluscs (Mann 1973; Teagle et al. 2017). The kelp forests shelter these plants and animals from the full force of the waves and influence water flow (Duggins et al. 1990). They also decrease the amount of light penetrating the water column and create a unique environment for species that prefer limited light conditions (Santelices and Ojeda 1984).

Kelp plants play a strong role in structuring the ecosystem and often act as a foundation species (Teagle et al. 2017), creating both primary and secondary habitat for invertebrates (Christie et al. 2003). Larger animals, such as crustaceans, then hunt the invertebrates, linking the trophic levels (Norderhaug et al. 2005). Since kelp forests play a vital role in creating new habitats, it is important to understand why they are under threat.

The main threats facing kelp forests are herbivory (typically from sea urchins) and human activities (Krumhansl 2016; Steneck et al. 2002). The main anthropogenic impacts are the result of climate change, diminished water quality and over-grazing, usually as a result of trophic cascades driven by overfishing (Brodie et al. 2014; Smale et al. 2013; Steneck et al. 2002; Steneck and Johnson 2013). Kelp beds are sensitive to disturbance and can disappear completely due to stressors such as strong storms, excessive herbivory and sudden rise in ocean temperature, but can also reappear in the same place almost as suddenly (Harrold and Reed 1985; Hart and Scheibling 1988; Scheibling 1984; Tegner et al. 1997; Witman 1988). Stronger and more

frequent storms, caused by climate change, may reduce the range and species diversity of kelp forests, leaving them more vulnerable to invasion by alien species (Edgar et al. 2004; Teagle et al. 2017).

Kelp forests occur in Southern Africa from Lüderitz in Namibia to Cape Agulhas, South Africa. The high nutrient levels, ample light exposure and continuous wave action along the western coast of South Africa provide an excellent environment for extensive kelp forests (Field et al. 1980). The large areas of kelp beds are vital to the inshore ecology of the west coast (Branch 1981). These kelp beds provide habitat for a large variety of flora and fauna with over 120 species found during a survey of the kelp beds along the coast of the southwest Cape (Field et al. 1980). Filter feeders such as mussels play an important role in moving energy up the food chain in these ecosystems, but due to the large swells in this area the role of sea-urchin grazing on kelp is minimal by comparison with other parts of the world (Field et al. 1980).

Four species of kelp occur in South Africa with *Ecklonia maxima* being the dominant species in shallow waters of the southwest coast of the continent but largely replaced by *Laminaria pallida* up the west coast (Branch et al. 2016). *E. maxima* has a thick holdfast that secures it in place, a hollow gas-filled stipe, which is a stem-like structure, and a bulb at the top that keeps it afloat. *E. maxima* is the largest of all kelp species found in southern Africa, reaching lengths up to 12 m and occurring at depths from about 0.5 to 15 m (Branch et al. 2016).

Kelp forests on many coasts have been important to humans living along the coastline for thousands of years providing an invaluable food source, through the kelp itself and the species it supports (Erlandson 2002; Simenstad et al. 1978). Globally, ecosystem services provided by kelp forests are valued at billions of dollars every year (Beaumont et al. 2008). They provide nursery grounds and habitat for a variety of species that are of commercial and conservation value (Holbrook et al. 1990: Smale et al. 2013; Steneck et al. 2002; Tegner and Dayton 2000), including abalone (*Haliotis midae*) in South Africa. Feed for commercial abalone farms is one of the main drivers behind kelp frond harvesting in much of the country and kelp is also a valued product in the seaweed industry (Rothman et al. 2006).

The seaweed industry began in South Africa in the early 1950s, when supplies of agar from Japan were suddenly cut off following World War II (Anderson et al. 1989; Isaac and

Molteno 1953). While several species of seaweed are harvested in South Africa, *E. maxima* is collected in the greatest quantities (Anderson et al. 2003). The kelp is harvested either through lethal harvesting of the whole plant, or via a non-lethal method where most but not all of the frond material is removed from the heads (Rothman et al. 2006). Due to the nature of kelp harvesting in South Africa, the growth of mussels on the kelp heads and stipes has the potential to impact upon both these harvesting processes.

Marine invasive species

The field of invasive species only began to gain attention as a scientific discipline in the 1980s (Reichard and White 2003), but today invasive species are recognised as posing a large and insidious threat to biodiversity globally, including in marine ecosystems (De Poorter et al. 2009). However, there is little research investigating how these introduced species alter the structure and function of the invaded biological community (Robinson et al. 2007) and how the level of impact is also determined by attributes of species in the invaded community interacting with the introduced species (Kumschick et al. 2014; Ricciardi et al. 2013).

Many invasive species are ecosystem engineers, substantially altering the physical structure and composition of invaded communities (Bax et al. 2003) and this is also the case in marine environments throughout the world (Grosholz 2002; Mack et al. 2000; Ruiz et al. 1999). Some marine invasive species have been introduced intentionally, dating back to the times of the Vikings (De Poorter et al. 2009). The American soft shell clam (*Mya arenaria*), for example, was intentionally brought from North America to northern Europe, most likely as a food source (De Poorter et al. 2009). However, the majority of marine invasive species have been accidentally spread through international shipping, with ballast water and hull fouling being the primary vectors for introductions (De Poorter et al. 2009).

The hulls of ships are filled with seawater, which is used as a ballast to stabilise the ship. As the ship travels to different ports, seawater is added or discharged to balance the ship, or as fuel is added or removed (De Poorter et al. 2009). In this way, species from multiple ports can be discharged all over the world (De Poorter et al. 2009). At any given time around 10,000 different species are potentially being transported across different biogeographic regions in the ballast water of ships (Carlton 2001).

As of 2016, there were 36 alien and 53 invasive marine species in South African waters, of which the Mediterranean mussel (*Mytilus galloprovincialis*) is the most ecologically significant and most intensively researched species (Alexander et al. 2016; Robinson et al. 2016).

Mytilus galloprovincialis in South Africa

M. galloprovincialis is an aggressive invader, which prefers cool-temperate waters, and has colonised many locations around the world, including South Africa (Branch and Steffani 2004). Originating from the Mediterranean, it was first detected in South African waters in 1984 (Grant et al. 1984), but only positively identified in 1985 (Grant and Cherry 1985). The mussel is unlikely to have been present much before the late 1970s (Griffiths et al. 1992), as it is not found in museum collections made prior to 1970 (De Moor and Burton 1988), nor in archaeological sites in the region (Grant and Cherry 1985). *M. galloprovincialis* was first observed on the west coast of South Africa in Saldanha Bay harbour, but it is not understood why the mussel first appeared there, instead of the much larger harbour in Cape Town (Branch and Steffani 2004), as ballast water was the likely vector for its arrival (Griffiths et al. 1992).

Currently, *M. galloprovincialis* is found from southern Namibia along the entire coastline of the Northern and Western Cape provinces of South Africa, and as far as East London in the Eastern Cape and has become the dominant mussel species in the area, outcompeting indigenous mussels *Choromytilus meridionalis* and *Aulacomya ater* (Assis et al. 2015). On the west coast the mussel accounts for 74% of all mussel biomass on exposed shorelines (Griffiths et al. 1992; Hockey and van Erkom Schurink 1992). The mussels are broadcast spawners that produce millions of larvae which drift long distances with ocean currents and wind (Branch and Steffani 2004). As a result, they can spread at a rate of up to 115 km per annum in a northerly direction every year, possibly following the Benguela Current up the west coast (Hockey and van Erkom 1992), however in the past decade the spread of the mussels appears to have halted (Assis et al. 2015). Mussels not only spread quickly but are ecosystem engineers which have the potential to radically modify their environment (Bax et al. 2003).

When mussels group together they form a complex bed, which protects them from predators and changing environmental conditions (Gosselin and Chia 1995; Robinson et al. 2007). This structure also creates a sheltered habitat for other species, which settle and develop

within the mussel matrix (Robinson et al. 2007). Their presence thus generally leads to an increase in species diversity and overall biomass in the ecosystem (Branch and Steffani 2004).

The introduction of *M. galloprovincialis* to South Africa has led to an overall increase in the standing stock of mussels along the coast (Griffiths et al. 1992), and has radically changed the ecosystems in the area (Robinson et al. 2007; Sadchatheeswaran et al. 2015). Their introduction has also led to an increase in food availability for predators such as the African black oystercatcher (*Haematopus moquini*) (Hockey and van Erkom Schurink 1992; Griffiths et al. 1992). This has had a positive impact on oystercatchers (Hockey and van Erkom Schurink 1992), likely helping them move from being near-threatened to a species of least concern on the IUCN Red List (BirdLife International 2017).

M. galloprovincialis has partially outcompeted local indigenous species due to its rapid growth rate, high tolerance to desiccation and high reproductive output and recruitment rate (Assis et al. 2015; Harris et al. 1998; Hockey and van Erkom Schurink 1992; van Erkom Schurink and Griffiths 1990; 1991; 1992). The mussel is, however, typically not found in the subtidal zone. The reason for this is unknown, as the mussels will grow on aquaculture ropes in the subtidal zone (Branch and Steffani 2004).

In 2016 *M. galloprovincialis* was first observed growing on *E. maxima* heads and stipes in False Bay in the Western Cape of South Africa (Foster C, *pers. comm.*). These mussel masses were also occasionally observed to reduce the buoyancy of the kelp sufficiently to topple the plants onto the sea floor, where the mussels were eaten by starfish (Foster C, *pers. comm.*). This is a novel phenomenon and has not been observed before. The invasive mussel masses are also creating a complex habitat on the stipes and heads of the kelp plants and it was expected that other species, that would not survive on the kelp plants otherwise, might colonise these mussel masses. This could also provide new habitat for other indigenous and invasive species, which could subsequently be spread long distances through kelp-rafting events.

Kelp rafting events

Kelp holdfasts frequently detach from the ocean floor, or the stipe breaks off the holdfast, as a result of strong storms or other disturbances, causing the detached plant to break free and drift away (Bushing 1994; McPeak et al. 1988; North 1991). When plant remains positively buoyant,

the kelp can drift vast distances with ocean currents and wind (Bushing 1994; Teagle et al. 2017). In the Southern Ocean, rafting events such as this are frequent (Smith 2002). It is possible these rafting events have played a significant role in marine species dispersal and colonisation in the past, as rafting events may help explain the distribution of some cosmopolitan species which appear to have limited dispersal ability (Bushing 1994; Dell 1972; Fell 1962; Fraser et al. 2011; Highsmith 1985; Ingólfsson 1995).

For floating kelp to act as a vector for the distribution of species it must persist long enough to transport species to other regions. Factors determining how long a drifting kelp plant will persist in the open ocean are wind patterns and ocean currents and population densities of grazing animals (Bushing 1994; Edgar 1987). As climatic conditions become more extreme, more kelp rafts may be transported across long distances, potentially spreading new species to areas that are already stressed from the effects of climate change (Edgar et al. 2004; Teagle et al. 2017).

There has been some evidence that invertebrates have been distributed vast distances on kelp rafts. Arnaud et al. (1976) found kelp, most likely *E. maxima,* which had drifted thousands of kilometres from South Africa to St. Helena Island in the southern Atlantic Ocean, nearly 2000 kilometres off the coast of Angola. They found 14 species of invertebrates on the kelp drifting around the island (Arnaud et al. 1976). The most abundant species were the Cape urchin (*Parechinus angulosus*), two species of brittle sea star (*Ophiuroidea*) and the ribbed mussel (*Aulacomya atra*) (Arnaud et al. 1976).

Aims and objectives

The overall aim of this project was to gain a better understanding of the ecological impacts of the invasive mussel *M. galloprovincialis* colonising the canopy of kelp forests (*E. maxima*) in False Bay. This project aimed to define the distribution and proportion of infected kelp within the kelp bed and determine the population structure of the mussels growing on the kelp. Other aims included determining how the mussels impact the buoyancy of the kelp plants. Finally, communities of organisms inhabiting the mussel masses on kelp heads and stipes were examined to see if these vary and whether the kelp canopy community has been altered due to the mussel infection. This in turn determines the extent to which mussel infected kelps could act as a transport vector for potentially invasive species.

To achieve these aims the objectives were:

- To first determine the distribution and proportion of infected kelp plants (kelp with mussels) and uninfected kelp plants (kelp without mussels) within the kelp bed and gain an understanding of how widespread this problem is in the study area.
- To determine if there is a correlation between the size of the kelp and the weight of the mussels growing on it. Additionally, to determine the population structure of the mussels on each individual plant by measuring the shell lengths of the mussels.
- To determine the reduction in buoyancy of the kelp plants from the weight of the mussel masses. Ultimately to determine how much reduction in buoyancy is required before the plant topples over and dies.
- To examine the fauna associated with mussels growing on the stipes and heads of the kelp plants. This is important for determining what species the kelp plants may transport during rafting events and the risk of them spreading potentially invasive species.

This project is a novel study on a phenomenon that has not been observed anywhere else in the world with this species of mussel. Invasive species pose a major threat to indigenous biodiversity, therefore it is important to gain a better understanding of the impact the invasive mussel *M. galloprovincialis* is having on kelp forest ecosystems in False Bay and its potential to spread invasive species.

Methods

Study site

All data for the study were collected in False Bay, Western Cape, South Africa (Figure 1). At the widest point False Bay is 30 km across, with the north coast almost entirely sandy and the east and west coasts flanked by steep rocky mountain ranges (Spargo 1991). False Bay has a Mediterranean climate, with warm dry summers, receives most of its rainfall during the cool winter months, and is subject to strong south-easterly winds, especially in summer (Spargo 1991). False Bay lies between the cold Benguela Current on the Atlantic side and the warm Agulhas Current, both of which influence sea surface temperatures, which range between 14 °C in winter and 18 °C in summer on average (Dufois and Rouault 2012).

Data were collected over six days at four locations along the west coast of False Bay. The locations were chosen due to anecdotal evidence that *M. galloprovincialis* were growing on kelp (*E. maxima*) plants in the area (Foster C, *pers. comm.*). Sampling sites were Miller's Point (34.1347 °S, 18.2824 °E) on 12 September 2017, 17 October 2017 and 22 December 2017 and Water's Edge (34.1141 °S, 18.2656 °E) on 19 October 2017. Data were also collected at Buffels Bay (34.1904 °S, 18.2738 °E) on 2 November 2017 and from Windmill Beach (34.1200 °S, 18.272 3 °E) on 3 November 2017. Data were collected during three independent sampling events. The first sampling event collected infected kelp heads and infected kelp stipes to investigate associated biota. The second sampling event was a survey of all four locations to determine the distribution and proportion of infected kelp heads and stipes within the kelp bed. The last sampling event measured the buoyancy of uninfected kelp plants.

Figure 1. Sampling locations in False Bay, Western Cape, South Africa. Map modified from Google Earth.

Collection of mussel/kelp samples

Sampling was conducted by four to six people, using a powered inflatable boat and SCUBA equipment when necessary. Two snorkelers looked for infected kelp plants, and a SCUBA diver cut them at the base of the stipe. A snorkeler then took the plants to the boat to be taken ashore. On the shore each kelp plant was laid flat, and the stipe length measured from the base of the head to the top of the holdfast. If mussel masses were present on the stipe the start and end point of each mussel mass was recorded, this information was then used to investigate where on the stipes the mussel masses typically occur. Infected stipe portions were then cut off and placed in pre-labelled sample bags. When the length of infected stipe exceeded 50 cm, a sub-sample 20 cm long was collected. For head samples the fronds and stipe were cut off and the entire infected head was removed and placed into a pre-labelled sample bag. After the samples were processed the remaining portion of the plant was discarded back into the sea. In total 20 infected heads and 17 infected stipe samples were collected from Miller's Point and three additional infected stipes were collected from Windmill Beach (as infected stipes were rare and hard to find). All samples were transported to the University of Cape Town, where they were frozen for later examination.

These samples were then used to investigate the biota living on infected kelp heads and stipes and to determine the mass, abundance and population structure of the mussels in each sample.

Density of infected kelps

At all four sample locations transect data were gathered during low spring tides to determine the distribution and proportion of infected and uninfected kelp plants within the kelp bed. At each site snorkelers swam from the shore to the outer edge of visible (surface-reaching) kelp, while placing floating 1 m^2 quadrats on the surface. The number of infected kelp heads and stipes, overall number of kelp plants, depth and distance from shore were recorded for each quadrat. A total of 279 quadrats were placed at the four sites, with one to five transects completed at each site. Two transects were completed perpendicular to the shore, spaced 30 m apart, from start of kelp bed to outer edge of visible kelp. Three transects were completed parallel to the shore, spaced 25 m apart, with the last transect taken across the outer edge of the kelp bed. A quadrat was taken every three meters and the number of quadrats per transect was determined by the length of transect, and varied from 10 to 33 quadrats. The total area surveyed (m^2) was also recorded for each site.

Kelp buoyancy

Kelp buoyancy data were collected at Miller's Point to determine the potential reduction in buoyancy as a result of the mussel masses and to investigate if stipe length had an effect on buoyancy. Divers collected 31 uninfected kelp plants across a full size range of plants (stipe lengths 121 to 599 cm), with their holdfasts still intact, and brought them to the shore team. The plants were laid out flat on the shore and their stipe lengths measured. The holdfasts were then cut off at the base of the stipe, where the stipe is still solid. The remaining kelp plant was then curled up and tied together with cord and its total mass measured using a spring balance. Each plant was then given back to the boat team to measure the buoyancy of the kelp plants when submerged in seawater. This was done by attaching a spring balance beneath the floating plant, then pulling downward on the balance from underwater until the plant was just submerged and taking a reading of the upward pull on the balance. The kelp was then discarded back in the bay.

Associated fauna and flora

The 20 infected head and 20 stipe samples were subsequently processed in the laboratory to determine the flora and fauna associated with each sample. Samples were individually thawed in

a large sorting tray containing seawater and all fauna and flora removed from the kelp stipe or head with a knife. *M. galloprovincialis* from each sample were first separated, rinsed in water and placed into a separate container. Any other flora and fauna associated with the sample was then separated into component species and identified under a dissecting microscope, to species level where possible, and abundance for each species recorded. All individuals of each species were then placed on a dry paper towel to remove excessive moisture, placed in a petri dish and total wet biomass (g) was then measured using a laboratory balance. A voucher specimen of each species was preserved in 90% isopropyl alcohol to be used as an identification guide. If any organism could not be identified by the author, it was forwarded to a relevant taxonomic expert for proper identification. Experts who assisted with identification included Dr Wayne Florence (Iziko South African Museum, Bryozoa), Prof Charles Griffiths (UCT, Amphipods and Isopods) and Prof Robert Anderson (UCT, seaweeds).

The shell lengths (mm) of the first 100 randomly selected *M. galloprovincialis* in each sample were measured using a Vernier caliper. The measurements were categorised into 10 mm increments to determine an age structure for the mussels in each sample. The wet mass of all *M. galloprovincialis* from each sample was recorded both in air and submerged in seawater. The wet mass in air was measured using a laboratory balance, while the submerged mass was measured with a spring balance by placing all the mussels in netting and submerging them in seawater. A few mussel masses were too small to determine submerged mass accurately with a spring balance, and in these cases a ratio calculated from the other measurements (0.33 g in sea water to 1 g in air), was applied to the wet mass in air. The submerged mass of mussels was later used to determine the potential reduction in buoyancy of the kelp plants caused by mussel masses.

Statistical Analysis

Statistical tests were performed on data using generalised linear models (GLM) in R (R Core Team 2017) using the car (Fox and Weisberg 2011), MASS (Venables and Ripley 2002) and MuMIn (Bartoń 2018) packages. All data (count and categorical) were plotted to check distribution and GLMs were performed with a Poisson specified error structure and a log link function (Table 1). All data were corrected for over-dispersal where necessary. An analysis of variance (ANOVA) test was performed after running each model to test for significance between explanatory variables. Each explanatory variable in the final model was determined using

ANOVA tables with Chi-squared tests. Predictor variables with $p < 0.05$ were immediately included in the model and predictor variables which did not contribute significantly ($p > 0.05$) were dropped from the model. The Akaike's Information Criterion (AIC) and Quasi Akaike's Information Criterion (QAIC) values of the full and final models were then compared to ensure that the final model was indeed a better fit than the full model (Zuur et al. 2009). When investigating the distribution of infected heads and stipes in relation to depth, when significant effects of depth were found, a pairwise comparison was run using the lsmeans package (Lenth 2016) to elucidate which depths were significantly different from each other.

Table 1. Statistical analysis using generalised linear models (GLM). *Models corrected for over dispersion when necessary. Infection rate is the percentage of infected kelp heads in areas surveyed within transects. Mussel mass is wet mass in air (g). Species richness is total number of species. Buoyancy is effort to pull kelp head underwater (-g). Depth and stipe length are measured in 100cm increments (e.g. 300-399 cm). All variables are continuous with the exception of stipe length and depth, which are categorical.

Model	Response	Explanatory	Distribution
GLM	Infection rate of kelp heads (%)	Depth	Poisson*
GLM	Mussel mass (heads)	Stipe length	Poisson*
GLM	Mussel mass (stipes)	Stipe length	Poisson*
GLM	Buoyancy	Stipe length	Poisson*
GLM	Species richness (heads & stipes)	Stipe length + Mussel mass	Poisson*
GLM	Species richness (heads)	Stipe length + Mussel mass	Poisson
GLM	Species richness (stipes)	Stipe length + Mussel mass	Poisson

Multivariate analyses of community data were performed using the vegan (Oksanen et al. 2017) and BiodiversityR (Kindt and Coe 2005) packages in R (R Core Team 2017). Species accumulation curves with 500 iterations were plotted to determine if enough head and stipe samples had been collected to adequately measure true biodiversity. Diversity, expressed by the Shannon-Wiener Index, which incorporates measures of both species richness and evenness, was calculated for each head and stipe samples to compare species diversity. A Welch Two Sample t-test was then run to determine if there were significant differences in diversity between head and stipe samples. Non-metric multidimensional scaling ordination using the Bray-Curtis index in the vegan package (Oksanen et al. 2017) was used to determine dissimilarity between head and stipe samples. A stress plot was created for all community data to determine goodness of linear fit using R^2 values. A permutational multivariate analysis of variance using distance matrices (PERMANOVA) was performed using the adonis function in the vegan package (Oksanen et al. 2017) to test for statistical differences between the biota found on head and stipe samples.

Lastly, community data collected from the study were compared against a study by Allen and Griffiths (1981), on the fauna and flora of a kelp bed canopy at Oudekraal, a site on the west coast of the Cape Peninsula. The community data were split by phyla into four groups; Mollusca, Crustacea, Polychaeta and 'other' (mainly Bryozoa, Hydrozoan and algae). The number of species for each category in the 1981 study was compared with this study to investigate differences in biological community composition. Due to the different sampling techniques and locations, a statistical comparison could not be made, therefore data were explored graphically in Microsoft Excel 2011.

Results

Substantial clumps of invasive mussel *M. galloprovincialis* were observed growing on both the stipes (Figure 2A) and heads (Figure 2B) of *E. maxima* at all the study sites visited along the western shores of False Bay. In some cases these were large enough to topple the kelp plants, leaving them lying horizontally on the sea floor and in such cases predatory starfish (*Marthasterias africana*) had congregated on the fallen kelps to feed on the mussels (Figure 2C). Various aspects of the mussel invasion are detailed in the subsections below.

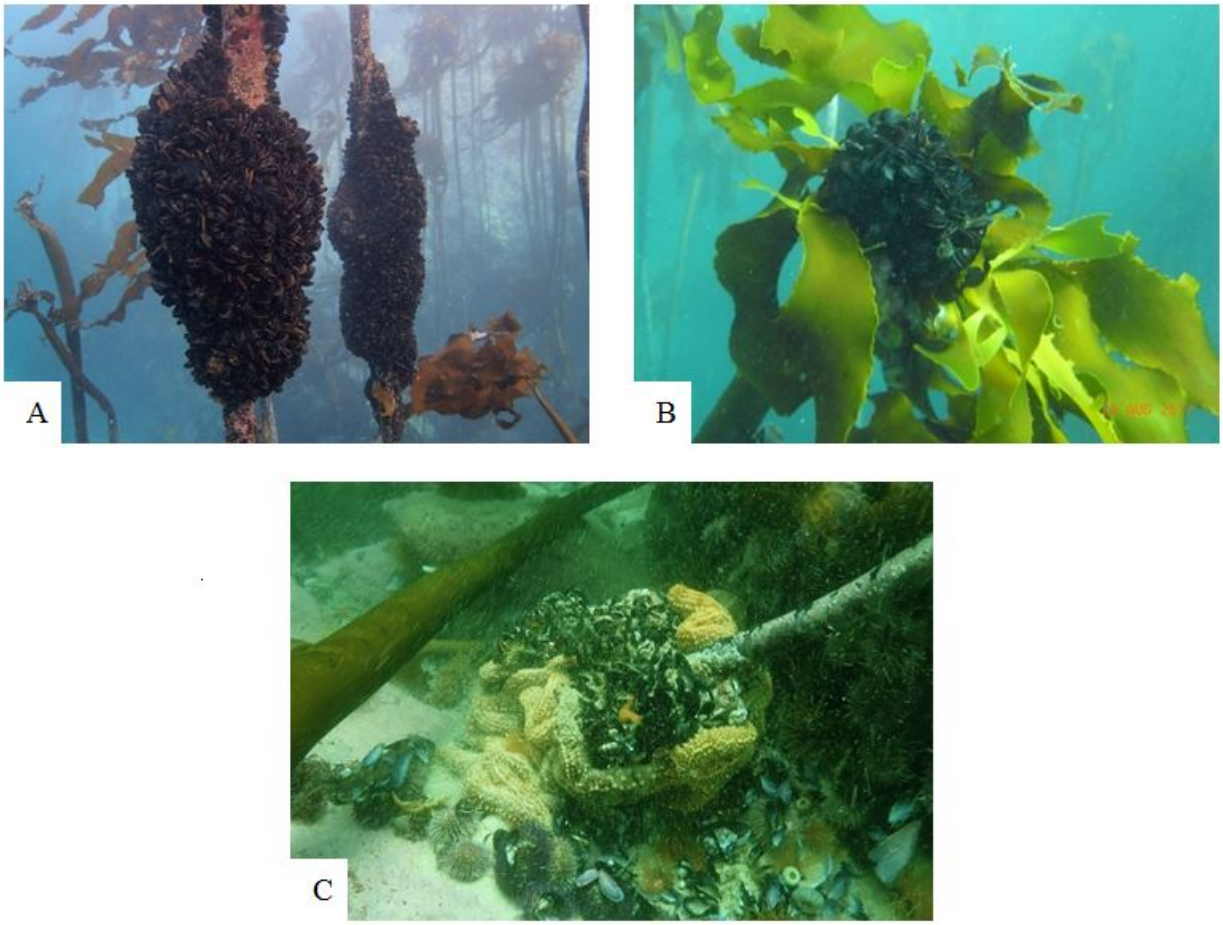

Figure 2. Mussel masses forming on A) kelp stipes (photo: Craig Foster) and B) kelp heads (photo: Robert Anderson) C) Mussel mass on toppled kelp head being eaten by starfish (*Marthasterias africana*) (Photo: Craig Foster).

Distribution and abundance of infected kelp plants

74 infected kelp heads were found in the 735 kelps examined during the transect survey. Infected kelp heads were absent from shallow water (< 200 cm) and became more common in deeper waters, especially at the outer edges of the kelp bed. By far the highest rates of infection were found at depths between 500 and 700 cm, where 40-45% of all kelps sampled had mussels on their heads (Figure 3). Infected kelp stipes were much rarer than infected kelp heads at any depth, with only two examples found in all transects (n = 735 kelps examined in total), one in the 500-559 cm depth range and one in the 300-399 cm depth range.

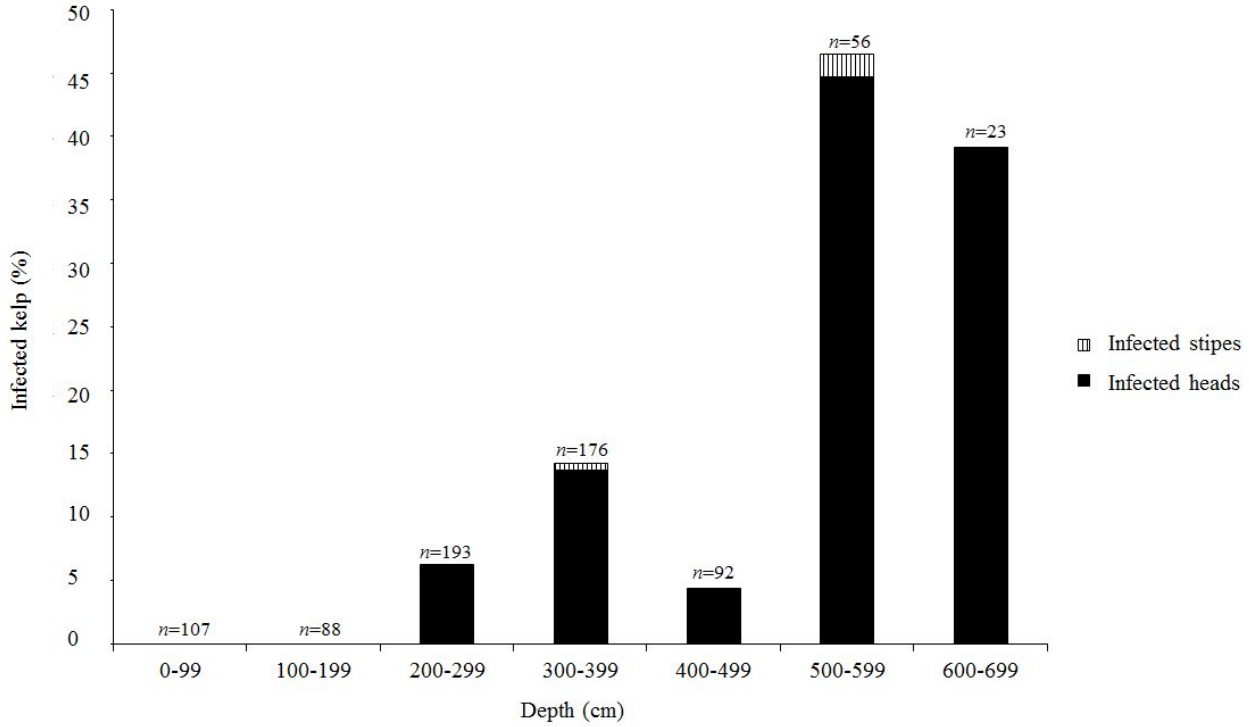

Figure 3. Average infection rate of kelp heads and stipes within four kelp beds in False Bay. Infected kelp (%) determined per depth category where n = total number of kelp surveyed in that depth range.

Although the density of kelp was generally lower in deeper waters, the proportion of infection was highest at depths between 500 and 700 cm (Table 2). A significant relationship was found between greater depths and increased kelp infection rate for heads ($p < 0.001$). Significant differences were found between depths 200-299 and 500-299 cm ($p < 0.001$), 200-299 and 600-699 cm ($p = 0.049$) and 300-399 and 500-599 cm ($p = 0.013$). No statistical tests could be applied to the infection rate of kelp stipes due to a sample size of two.

Table 2: Frequency and distribution of infected kelp heads and stipes in relation to water depth.

Depth range (cm)	Area surveyed (m^2)	Mean kelp density/m^2	Infected heads/m^2	Infected stipes/m^2
0-99	31	3.45	0	0
100-199	25	3.52	0	0
200-299	80	2.26	0.15	0
300-399	82	1.85	0.29	0.01
400-499	23	3.83	0.17	0
500-599	26	1.19	0.96	0.04
600-699	12	1.17	0.75	0

Relationship between mussel mass and stipe length amongst head samples

No significant relationship was found between the mass of *M. galloprovincialis* on kelp heads and kelp stipe length ($p = 0.175$). There is a trend of increasing variation in mussel mass on kelps with longer stipes, which grow in deeper waters (Figure 4).

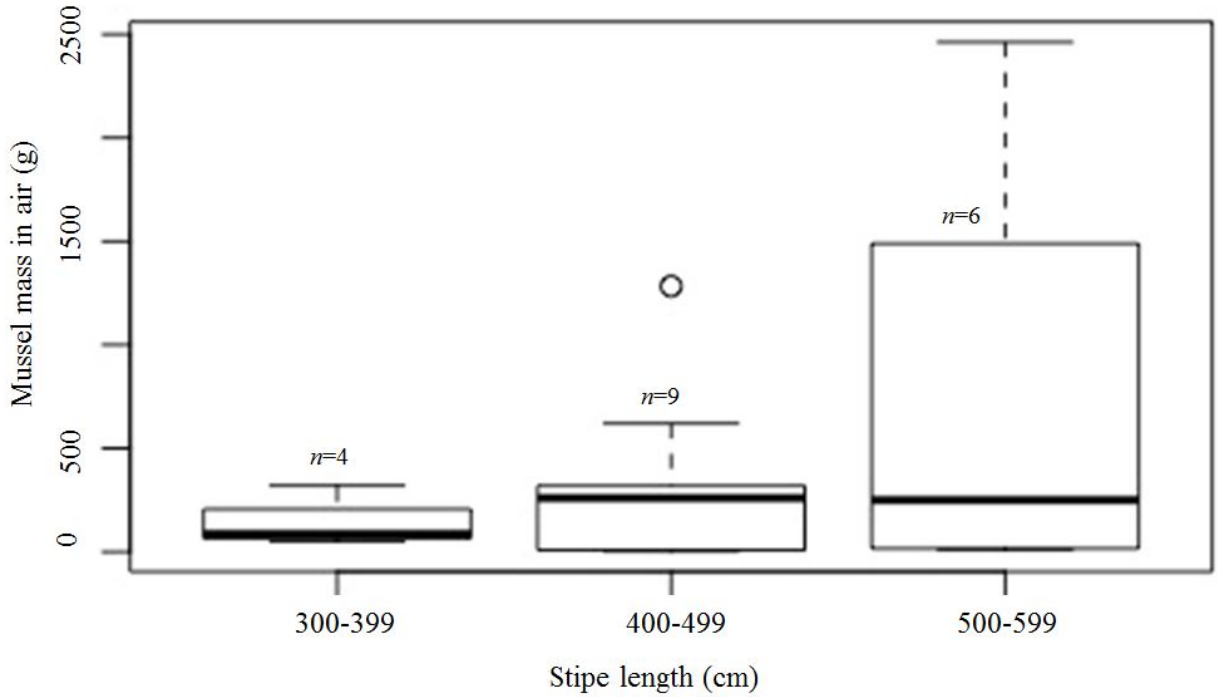

Figure 4. Wet mass of mussels in air (g) in relation to stipe length (cm) for heads. Stipe lengths 200-299 cm removed due to sample size of one. Boxes indicate entire interquartile range, the thick black line is median, the bottom of box is 25th percentile and the top of box is 75th percentile. The top whisker is 75% + 1.5 * interquartile range, the bottom whisker is 25% - 1.5 * interquartile range and small circles represent outliers.

There was little variation in the 300-399 cm and 400-499 cm range, however, a large amount of variation occurred in the 500-599 cm range with the largest mussel mass on head samples (2462 g) found in that range. No kelps with stipes less than 200 cm were observed to be

infected. Kelps with stipe lengths of 200-299 cm were removed from this analysis due to small sample size of one.

Table 3. Statistical analyses using generalised linear models (GLM). **Bolded** P values indicate significance. * Denotes variables that were removed in a stepwise fashion from the model if they were found not to have a significant effect on the response variable. Values for removed variables were generated before the variable was removed. Mussel mass is wet mass in air (g). Infection rate is the percentage of infected kelp heads in areas surveyed within transects. Mussel mass is wet mass in air (g). Species richness is total number of species. Buoyancy is effort to pull kelp head underwater (-g). Depth and stipe length are measured in 100 cm increments (e.g. 300-399 cm). All variables are continuous with the exception of stipe length and depth, which are categorical. Df is degrees of freedom and χ^2 refers to Chi-squared.

Model	Response variable	Explanatory variable	Df	χ^2	P Value
GLM	Infection rate of kelp heads (%)	Depth	6,246	36.938	**<0.001**
GLM	Mussel mass (heads)	Stipe length	2,16	3.484	0.175
GLM	Mussel mass (stipes)	Stipe length	3,16	1.698	0.637
GLM	Buoyancy	Stipe length	1,29	47.724	**<0.001**
GLM	Species richness (heads & stipes)	Stipe length*	4,34	7.838	0.098
		Mussel mass	1,38	8.864	**0.003**
GLM	Species richness (heads)	Stipe length*	3,15	5.014	0.171
		Mussel mass	1,18	5.674	**0.017**
GLM	Species richness (stipes)	Stipe length	3,16	8.109	**0.044**
		Mussel mass*	1,15	1.896	0.169

Relationship between mussel mass and stipe length amongst stipe samples

No significant relationship was found between the mass of *M. galloprovincialis* on kelp heads and kelp stipe length ($p = 0.637$). Stipe lengths of 600-699 cm showed the highest variability with the largest mussel mass found in this range (Figure 5).

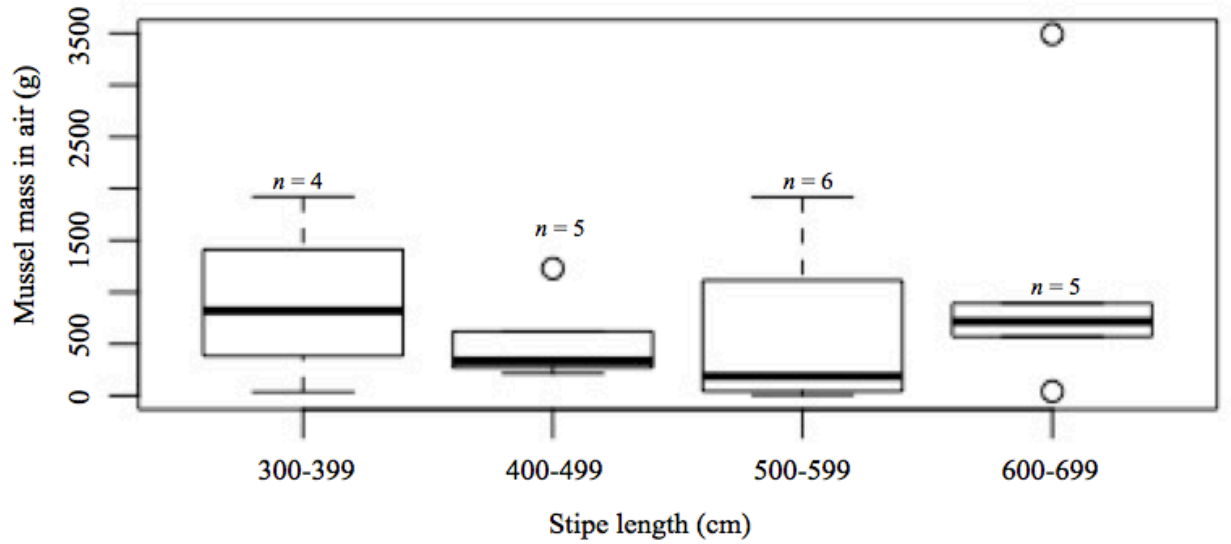

Figure 5. Wet mass of mussels in air (g) in relation to stipe length (cm) on stipe samples. Boxes indicate entire interquartile range, the thick black line is median, the bottom of box is 25th percentile and the top of box is 75th percentile. The top whisker is 75% + 1.5 * interquartile range, the bottom whisker is 25% - 1.5 * interquartile range and small circles represent outliers.

Position of mussel masses on stipe

Mussels were found all along the length of the kelp stipe from 20 cm above the holdfast to 460 cm above the holdfast, with the highest percentage of mussel masses found at 220 cm (45%). More than half (53%) of all mussel masses occur in the mid portion of the stipes 150-250 cm from the base (Figure 6).

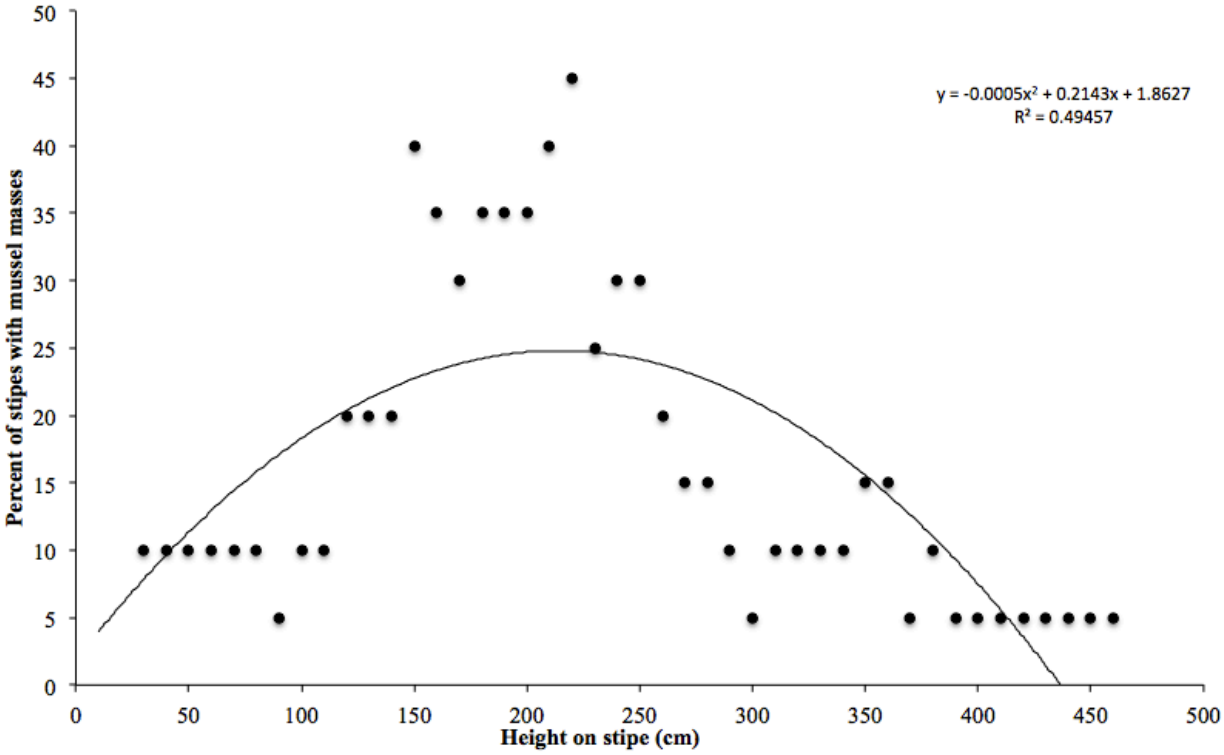

Figure 6. Position of mussel masses versus distance up stipes, measurements begin at the top of the holdfast.

Population structure of mussels on kelp plants

Mussels on both heads and stipes had a similar population structure with most individuals being smaller than 40 mm, and none larger than 90 mm (Figure 7).

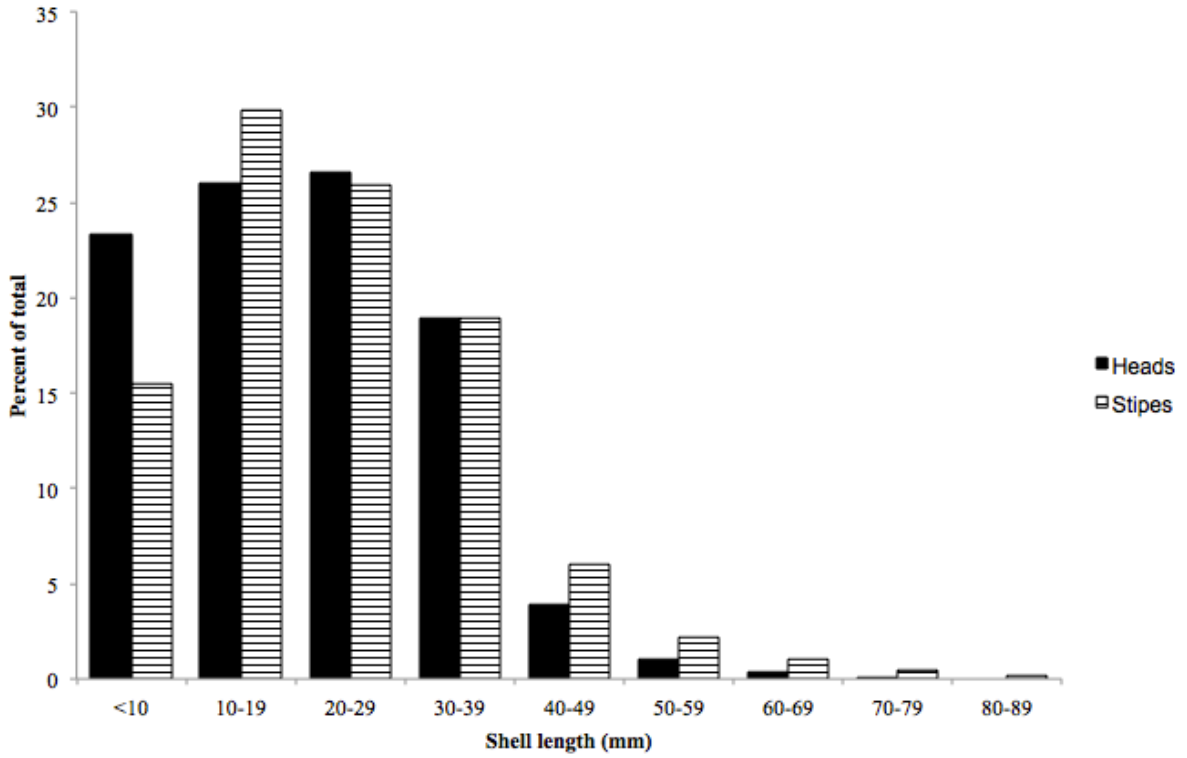

Figure 7. Population structure of *M. galloprovincialis* on infected kelp plants.

Head samples had a greater proportion of small mussels than stipe samples. On heads the most common shell lengths were 10-19 mm and 20-29 mm (both about 25% of total), with those below 10 mm also comprising over 20% of the total. Overall there was a slightly higher proportion of larger mussels (> 40 mm) on stipes than on kelp heads.

The total biomass of mussels found on head samples ranged from 2.5 to 2462 g, with a median (interquartile range) of 86.4 g (14.8 to 353.8 g). The total biomass of mussels found on stipes ranged from 7.6 to 3492 g, with a median of 595.5 g (194.0 to 955.0 g). Both head and stipe samples showed a large variation within the masses with stipes having a higher median than head samples. Of the five largest mussel masses collected three were from stipe samples and two from heads.

Buoyancy

The stipe lengths of the 31 kelp plants collected for measurement of buoyancy ranged from 121 to 559 cm. There was a significant positive relationship ($p < 0.001$) between increasing stipe length and increasing buoyancy, with the smallest plant having positive buoyancy of only 50 g and the largest plant a buoyancy of 3000 g. The relationship between buoyancy and stipe length was fitted to a power curve with the equation Buoyancy (g) = $127.45e^{0.0049}$ stipe length (cm). Kelp plants between 500 and 600 cm showed a large amount of variation in buoyancy with the highest buoyancy (3000 g) nearly triple the lowest (1100 g) (Figure 8).

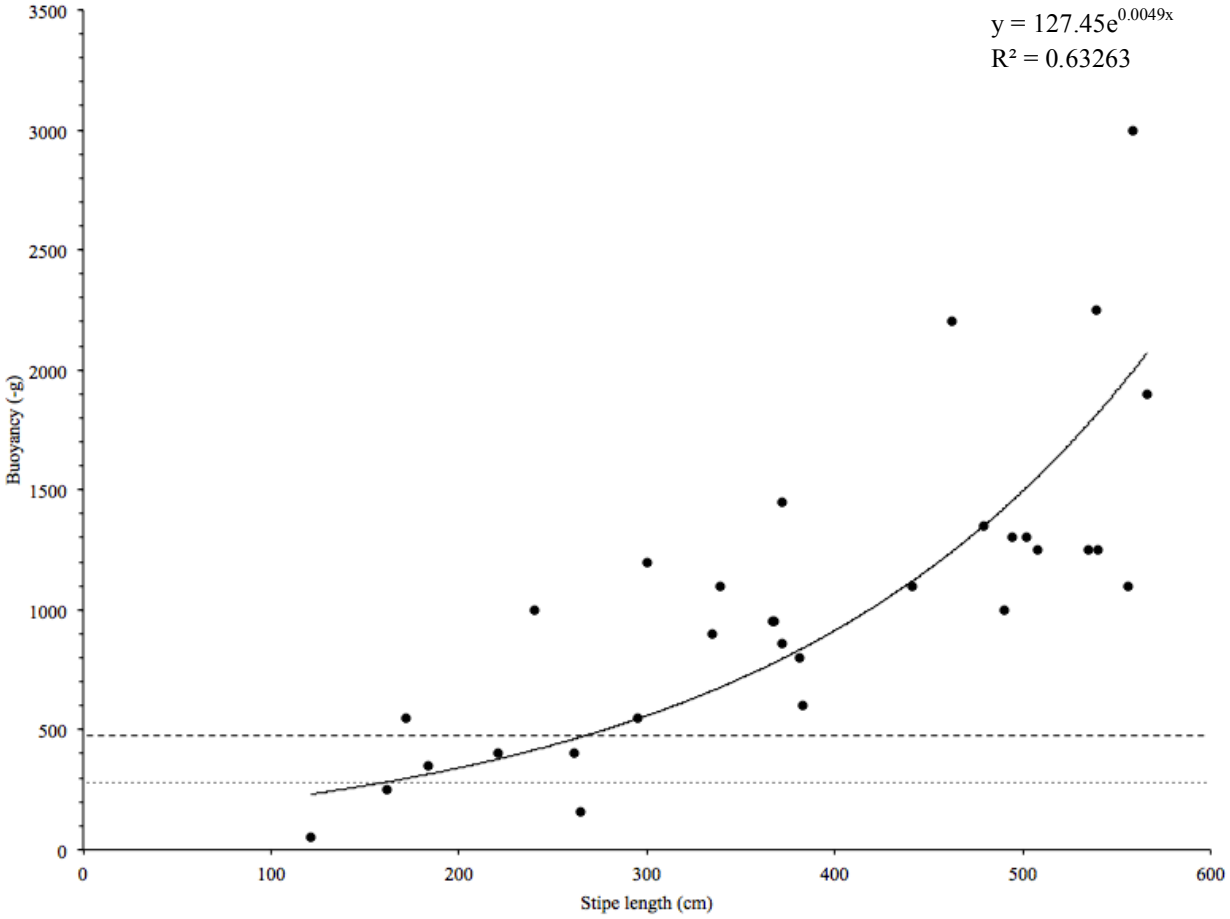

Figure 8. Buoyancy of 31 uninfected kelp plants. Dashed line indicates the median (interquartile range) of the five largest mussel masses on stipes of -490 g (-413 to -560 g), small dotted line indicates the median (interquartile range) of the five largest mussel masses on heads of -295 g (-150 to -305 g). Both mussel mass values were measured submerged in seawater (g).

The potential reduction in buoyancy indicated by the dashed and dotted lines shows that the median weight of the five largest mussel masses recorded on stipes and heads would have resulted in negative buoyancy in six (19.4%) and three (9.7%) kelp plants respectively, causing them to sink.

Fauna and flora associated with mussel masses

The total number of species recorded in head samples was 41, while 86 species were recorded in stipe samples. The most common taxon of species recorded in head samples was Mollusca and Crustacea each with nine species and Polychaeta (eight species), which together accounted for 63% of all of the species recorded on heads. The most common species in stipe samples were Polychaeta (15 species), Mollusca (15 species) and Crustacea (14 species), which together accounted for 51% of all species recorded on stipes.

Overall mean biomass (1177.034 ± 81.686 g) and mean number of individuals (1633.800 ± 84.524) for stipes samples were much higher than head samples (398.411 ± 40.430 g and 517.950 ± 44.165 respectively) (Table 4). On head samples the species with the highest mean biomass (392.048 ± 641.087 g) was *M. galloprovincialis*, followed by followed by the white dwarf barnacle (*Notomegabalanus algicola*) (1.013 ± 1.051 g) and then the ascidian red bait (*Pyura stolonifera*) (0.911 ± 3.462 g). *M. galloprovincialis* also had the highest mean number of individuals for head samples (427.550 ± 837.733), followed by the white dwarf barnacle (28.700 ± 23.261) and the Bryozoa *Cellporella hyalina* (17.050 ± 23.103 colonies). On stipe samples *M. galloprovincialis* had the highest overall mean biomass (771.719 ± 861.181 g) followed by the split fan kelp (*Laminaria pallida*) (177.712 ± 570.050 g), which was only found on stipe samples and red bait (69.630 ± 136.809 g). *M. galloprovincialis* had the highest mean number of individuals for stipe samples (710.450 ± 624.072) with the white dwarf barnacle (300.200 ± 673.829) and the tiny Polychaeta *Spirorbis sp*. (286.500 ± 395.501) following (Table 4).

Table 4. Species found on kelp heads and stipes. *Indicates species recorded in colonies, **bold** indicates alien species. Mean # refers to mean number of individuals, ± values are the standard deviation of the mean.

Group	Species	Mean biomass (g) (heads)	Mean # (heads)	Mean biomass (g) (stipes)	Mean # (stipes)
Porifera	*Sycon sp.*	0.096 ± 0.341	0.550 ± 2.235	0.428 ± 1.519	3.200 ± 7.964
Actinaria	*Anthothoe stimpsonii*			0.308 ± 1.290	0.500 ± 1.821
Actinaria	*Bunodosoma capense*	0.356 ± 1.007	0.650 ± 1.694	0.106 ± 0.269	0.350 ± 0.988
Hydrozoa	*Aglaophenia pluma*			0.230 ± 1.029	5.000 ± 22.361
Hydrozoa	*Bicorona elegans**	0.464 ± 1.567	1.150 ± 2.601		
Hydrozoa	Creeping hydroid sp.*	0.015 ± 0.067	0.050 ± 0.224		
Hydrozoa	***Halocordyle disticha****	**0.003 ± 0.010**	**0.150 ± 0.489**		
Hydrozoa	*Obelia dichotoma**	0.050 ± 0.224	0.050 ± 0.224	0.085 ± 0.285	1.050 ± 4.466
Hydrozoa	*Plumularia setacea**	0.022 ± 0.098	0.500 ± 2.236		
Hydrozoa	*Sertularella arbuscula**			0.109 ± 0.488	0.300 ± 1.342
Platyhelminthes	*Planocera gilchristi*			0.142 ± 0.343	1.200 ± 4.008
Nemertea	*Amphiporus sp.*	0.001 ± 0.003	0.200 ± 0.696	0.001 ± 0.003	0.100 ± 0.308
Polychaeta	*Dodecaceria pulchra*			0.015 ± 0.024	3.100 ± 6.585
Polychaeta	*Eunice sp.*	0.014 ± 0.060	0.050 ± 0.224	0.212 ± 0.718	0.550 ± 1.276
Polychaeta	*Filograna implexa*			0.590 ± 1.180	112.500 ± 225.000
Polychaeta	*Hemilepidia erythrotaenia*			0.011 ± 0.032	0.150 ± 0.489
Polychaeta	*Hesionidae*			0.001 ± 0.002	0.050 ± 0.224
Polychaeta	*Lepidonotus semitectus*	0.582 ± 0.854	3.850 ± 5.274	3.224 ± 3.106	40.650 ± 38.431
Polychaeta	*Loimia medusa*	0.181 ± 0.496	1.050 ± 2.964	2.340 ± 3.430	13.400 ± 15.059
Polychaeta	*Nereid sp.* (barred paragnaths)	0.035 ± 0.154	0.050 ± 0.224		
Polychaeta	*Nereid sp.* (no paragnaths)	0.031 ± 0.132	0.300 ± 1.129	0.011 ± 0.036	0.400 ± 1.188
Polychaeta	*Nereid sp.* (fluffy gills)			0.052 ± 0.234	0.300 ± 1.342
Polychaeta	*Nereid spp.*	0.014 ± 0.060	0.150 ± 0.489	0.062 ± 0.112	1.800 ± 3.254
Polychaeta	*Nereis sp.*			0.157 ± 0.529	2.900 ± 7.752
Polychaeta	*Pseudobranchiomma longa*			0.777 ± 1.526	2.400 ± 5.798
Polychaeta	*Serpula vermicularis*			0.192 ± 0.440	2.100 ± 5.291
Polychaeta	*Spirorbis sp.*	0.101 ± 0.129	16.300 ± 18.371	1.433 ± 1.978	286.500 ± 395.501
Polychaeta	*Syllis sp.*	0.006 ± 0.013	0.400 ± 0.883	0.033 ± 0.033	3.100 ± 3.447
Crustacea	*Amaryllis macrophthalma*			0.012 ± 0.038	0.600 ± 1.698
Crustacea	*Caprella equilibra*			0.002 ± 0.007	0.400 ± 1.569
Crustacea	***cf Melita oba***			**0.008 ± 0.015**	**0.750 ± 1.500**

Crustacea	*Cirolana cranchii*	0.001 ± 0.002	0.050 ± 0.224	0.071 ± 0.282	3.750 ± 16.078
Crustacea	*Cirolana sulcata*			0.026 ± 0.056	1.550 ± 3.284
Crustacea	*Cymodocella pustulata*	0.031 ± 0.059	5.600 ± 9.372	0.003 ± 0.004	0.300 ± 0.571
Crustacea	*Guinusia chabrus*	0.092 ± 0.209	0.500 ± 1.147	0.072 ± 0.189	0.400 ± 1.046
Crustacea	*Janira sp.*	0.001 ± 0.002	0.300 ± 1.342	0.001 ± 0.002	0.050 ± 0.224
Crustacea	*Lemboides spp.*	0.001 ± 0.002	0.350 ± 1.565	0.003 ± 0.013	0.300 ± 1.342
Crustacea	*Leucothoe richiardi*			0.001 ± 0.004	0.050 ± 0.224
Crustacea	*Notomegabalanus algicola*	1.013 ± 1.051	28.700 ± 23.261	10.668 ± 21.65	300.200 ± 673.829
Crustacea	*Paramoera capensis*	0.003 ± 0.004	0.400 ± 0.821	0.004 ± 0.011	0.400 ± 1.188
Crustacea	*Peramphithoe sp.*	0.005 ± 0.014	0.300 ± 0.733		
Crustacea	*Pilumnoides rubus*			0.058 ± 0.115	0.500 ± 1.000
Crustacea	*Tanais sp.*	0.003 ± 0.005	1.050 ± 2.114	0.001 ± 0.002	0.050 ± 0.224
Bryozoa	*Amphiblestrum sp.*			0.010 ± 0.045	0.200 ± 0.894
Bryozoa	*Bryozoan sp.* on coralline algae*			0.001 ± 0.006	0.150 ± 0.671
Bryozoa	***Bugula sp.****			**0.102 ± 0.293**	**1.100 ± 4.038**
Bryozoa	*Celleporaria capensis*			0.085 ± 0.170	0.750 ± 1.500
Bryozoa	*Cellporella hyalina**	0.665 ± 0.912	17.050 ± 23.103	0.101 ± 0.246	4.300 ± 11.448
Bryozoa	*Chaperiopsis sp.*			0.106 ± 0.306	0.850 ± 2.412
Bryozoa	*Gigantopora polymorpha*			0.238 ± 0.475	2.500 ± 5.000
Bryozoa	*Menipea crispa*			0.565 ± 1.130	0.500 ± 1.000
Bryozoa	*Pale ringed sp.**	0.040 ± 0.179	2.000 ± 8.944		
Bryozoa	*Schizoretepora tessellata*			0.150 ± 0.300	0.250 ± 0.500
Bryozoa	*Schizosmittina lizzya**			0.003 ± 0.011	0.100 ± 0.447
Bryozoa	*Turbicellepora cylindriformis**			0.076 ± 0.338	0.150 ± 0.671
Bryozoa	***Virididentula dentata****			**0.692 ± 2.106**	**0.650 ± 1.496**
Bryozoa	***Watersipora subtorquata****	**0.307 ± 0.457**	**4.050 ± 7.156**	**0.246 ± 1.035**	**0.800 ± 2.167**
Mollusca	*Anomia achaeus*	0.005 ± 0.018	0.250 ± 0.716	0.168 ± 0.244	5.800 ± 7.502
Mollusca	*Aulacomya atra*	0.012 ± 0.024	0.350 ± 0.671	1.354 ± 1.421	11.900 ± 14.628
Mollusca	*Chiton politus*			0.823 ± 3.681	0.300 ± 1.342
Mollusca	*Crepidula porcellana*	0.004 ± 0.013	0.100 ± 0.308	1.422 ± 6.247	2.850 ± 12.049
Mollusca	*Cymbula compressa*	0.273 ± 0.802	0.750 ± 1.020	0.005 ± 0.015	0.550 ± 1.572
Mollusca	*Fissurella mutabilis*	0.003 ± 0.013	0.050 ± 0.224	0.446 ± 0.971	3.450 ± 6.186
Mollusc	*Godiva quadricolor*	0.027 ± 0.087	0.100 ± 0.308		
Mollusca	*Helcion pruinosus*			0.009 ± 0.040	0.100 ± 0.447
Mollusca	*Hiatella arctica*			0.730 ± 1.281	11.900 ± 21.494
Mollusca	*Kellia rotunda*	0.006 ± 0.016	0.250 ± 0.550	0.069 ± 0.150	3.150 ± 6.011
Mollusca	*Limaria tuberculata*			0.111 ± 0.422	0.600 ± 1.847
Mollusca	*Musculus cuneatus*	0.001 ± 0.002	0.050 ± 0.224	0.021 ± 0.055	0.450 ± 1.395

Mollusca	***Mytilus galloprovincialis***	**392.048 ± 641.087**	**427.550 ± 837.733**	**771.719 ± 861.181**	**710.450 ± 624.072**
Mollusca	*Oxystele sinensis*			9.480 ±18.960	1.500 ± 3.000
Mollusca	*Talochlamys multistriata*			0.053 ± 0.235	0.400 ± 1.789
Mollusca	*Turbo cidaris*			37.830 ± 75.660	1.500 ± 3.000
Echinodermata	*Comanthus wahlbergii*			0.015 ± 0.030	1.500 ± 3.000
Echinodermata	*Parechinus angulosus*	0.219 ± 0.642	1.100 ± 2.751	0.759 ± 2.088	4.200 ± 10.103
Echinodermata	*Pentacta doliolum*			0.100 ± 0.200	2.750 ± 5.500
Echinodermata	*Pseudocnella insolens*			0.043 ± 0.085	0.250 ± 0.500
Echinodermata	*Thyone aurea*			0.056 ± 0.166	1.500 ± 5.385
Ascidiacea	*Ascidia canaliculata*			15.272 ± 52.017	6.500 ± 11.985
Ascidiacea	*Botryllus magnicoecos*	0.770 ± 1.619	0.650 ± 0.988	31.452 ± 50.428	9.100 ± 26.501
Ascidiacea	*Pyura stolonifera*	0.911 ± 3.462	0.250 ± 0.716	69.630 ± 136.809	3.850 ± 5.499
Chlorophyta	*Chaetomorpha sp.*			0.003 ± 0.012	0.250 ± 1.118
Chlorophyta	*Cladophora capensis**			0.121 ± 0.358	0.850 ± 2.084
Chlorophyta	*Codium lucasii*			0.860 ± 2.680	1.500 ± 4.072
Ochrophyta	*Ecklonia maxima*			8.998 ± 36.069	0.150 ± 0.489
Ochrophyta	*Exallosorus harveyanus*			1.875 ± 4.381	3.100 ± 6.086
Ochrophyta	*Laminaria pallida*			177.712 ± 570.050	1.100 ± 1.651
Rhodophyta	*Acrosorium maculatum*			0.011 ± 0.041	0.150 ± 0.489
Rhodophyta	*Arthrocardia sp.**			18.088 ± 46.338	16.050 ± 34.502
Rhodophyta	*Ceramium arenarium*			0.005 ± 0.022	0.100 ± 0.447
Rhodophyta	*Champia compressa*			0.015 ± 0.067	0.100 ± 0.447
Rhodophyta	*Phymatolithon foveatum**	0.009 ± 0.011	0.700 ± 0.733	3.873 ± 9.326	21.550 ± 42.721
Rhodophyta	*Plocamium maxillosum**			0.085 ± 0.265	1.050 ± 4.019
Rhodophyta	*Pterosiphonia cloiophylla*			0.006 ± 0.027	0.100 ± 0.447
Total	**94 spp.**	**398.411 ± 40.430 g of 41 spp.**	**517.950 ± 44.165**	**1177.034 ± 81.686 g of 86 spp.**	**1633.800 ± 84.524**

Of the 94 species found on heads and stipes, six were alien species known to occur in the Western Cape; these being *M. galloprovincialis* (invasive), three Bryozoans; *Watersipora subtorquat*a (invasive), *Viridid*e*ntula dentata* and *Bugula sp*., an Amphipod *Melita oba* and the

Hydrozoa *Obelia dichotoma*. A new un-described species of Amphipod (*Peramphithoe n. sp.*), which burrows into the heads of large kelps, was also discovered during the course of this study.

Species richness in relation to mussel mass

Species richness (total species) showed an increasing trend in relation to mussel masses for head and stipe samples combined ($p = 0.003$), with larger mussel masses having a higher species richness overall.

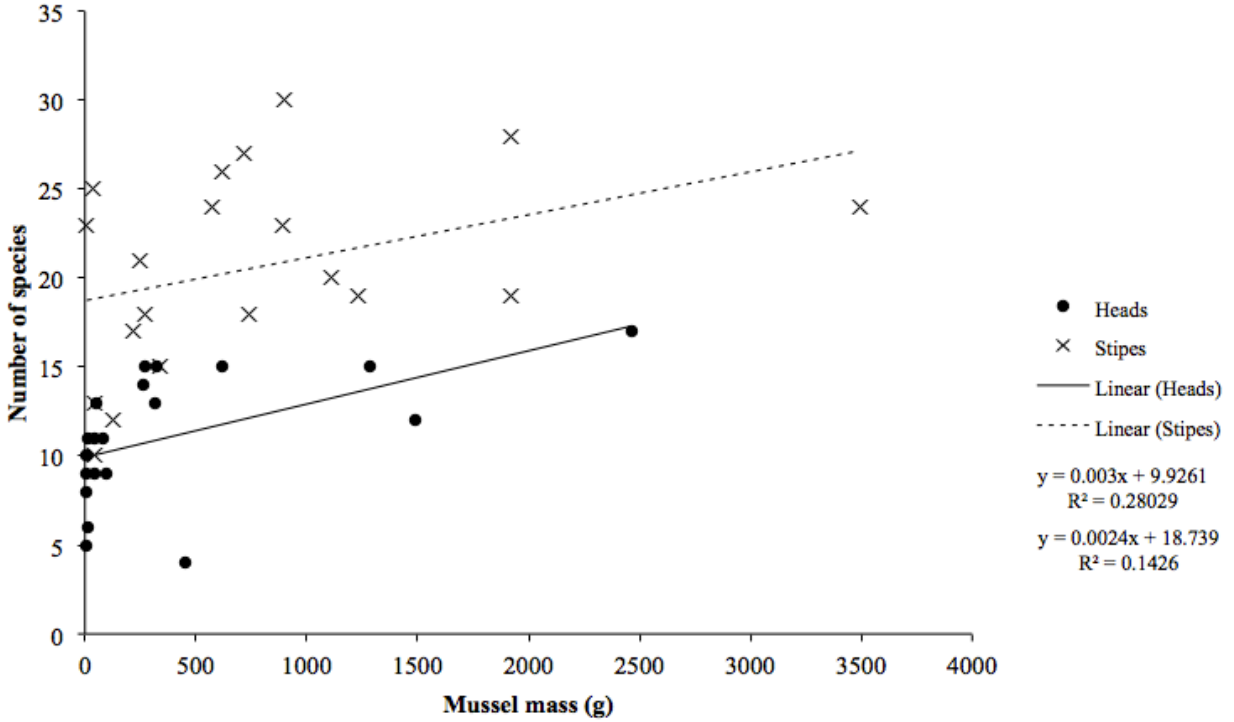

Figure 9. Mussel masses in relation to number of species (species richness) for head and stipe samples.

When head and stipe samples were modelled independently, mussel mass was found to have a significant effect on species richness for head samples ($p = 0.017$), with larger mussel masses having greater species richness (Figure 9). Mussel mass did not have an effect on species richness for stipe samples ($p = 0.169$). Stipe length however had a significant effect on species richness for stipe samples ($p = 0.044$), pairwise comparisons between stipe lengths showed that stipe lengths 300-399 cm had significantly more species than stipe lengths 500-599 cm ($p = 0.042$). All other pairwise comparisons between stipe lengths were not significant (all $p > 0.192$).

Species accumulation curves

Species accumulation curves again showed that stipe samples were more diverse than head samples in terms of number of species per sample collected (Figure 10). The curves indicate a relatively effective sampling level for kelp heads, with the curve approaching the asymptote after 20 samples. However, more stipe samples would be needed to approach a full complement of species in this habitat, as the number of species was still increasing after 20 samples.

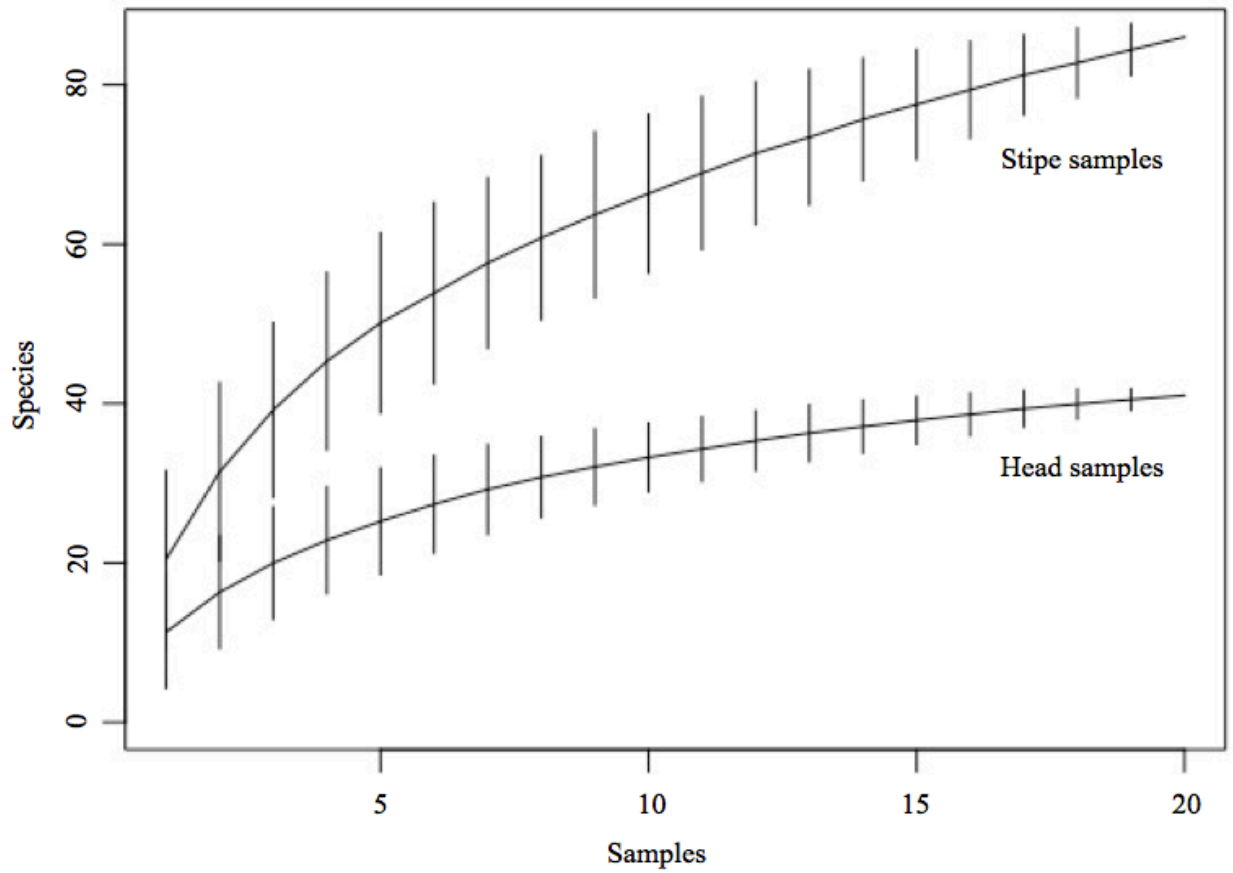

Figure 10. Species accumulation curves for head and stipe samples. Curve generated in R using 500 random iterations of samples collected at Miller's Point and Windmill Beach.

Stipe samples also had a higher Shannon's diversity index (1.78) than head samples (0.85), despite the head samples showing more variation in diversity between samples. The difference between the values was not statistically significant ($p = 0.341$).

Sample ordination

An NMDS ordination plot, showing dissimilarity of samples in terms of their species composition, is shown in Figure 11. The results of the PERMANOVA found a significant difference in the biota found on head and stipe samples ($p = 0.018$).

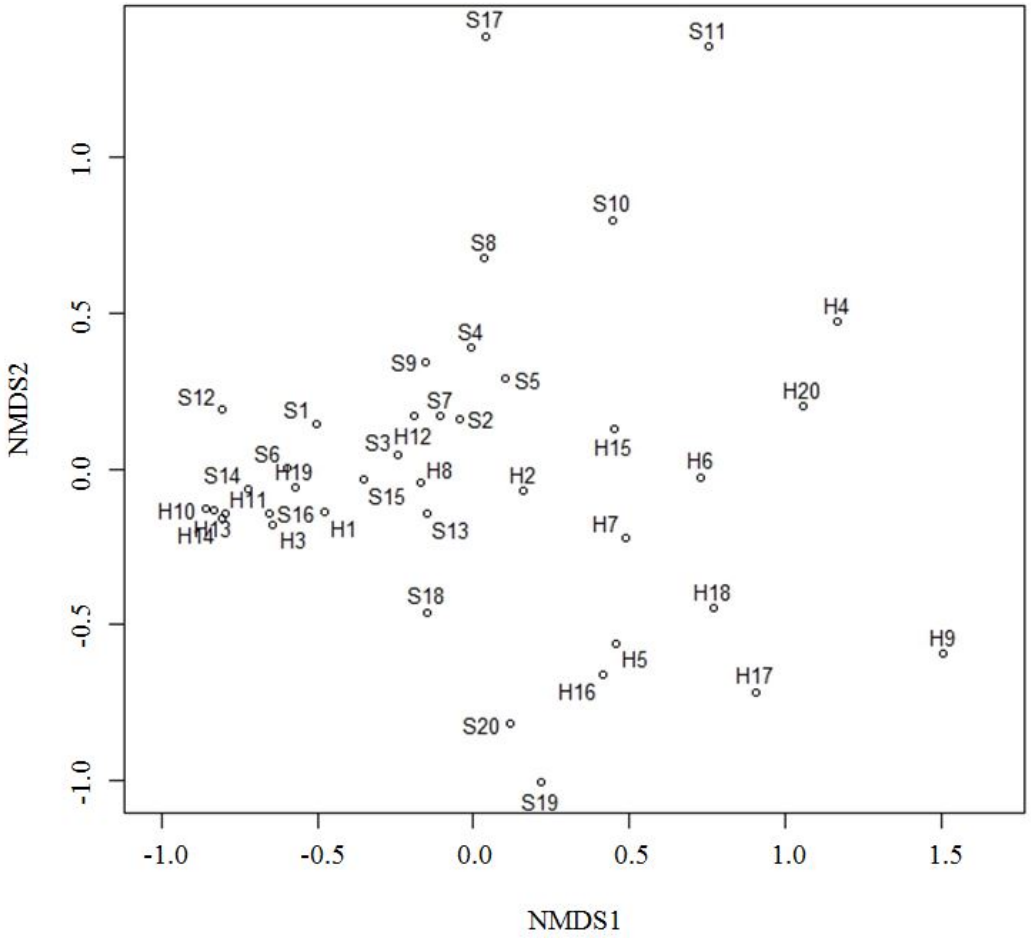

Figure 11. Non-metric multidimensional scaling (NMDS) ordination plot of head (H) and stipe (S) samples.

Groupings of similar head samples and groupings of similar stipe samples were found with many species found in both head and stipe samples. There were also several outliers with S17 and S11 being more dissimilar than other samples. Stress plots were created looking for goodness of linear fit of the ordination plots. The R^2 values of the stress plots were 0.83 for both heads and stipes samples, 0.89 for head samples and 0.87 for stipe samples, which are all a good fit for ecological data collected as part of an uncontrolled experiment.

Discussion

Although *M. galloprovincialis* was introduced to South Africa more than 35 years ago and has subsequently spread to become a dominant component of the rocky shore biota over more than 1500 km of coastline (Griffiths et al. 1992), it was only in 2016 that it was first observed growing on the heads and stipes of kelps (*E. maxima*) (Foster C, *pers. comm.*). The aim of this study was to determine the distribution patterns and possible ecological impacts of *M. galloprovincialis* colonising kelp forests in False Bay. The mussels were observed at all four of the study sites examined in False Bay, where *M. galloprovincialis* colonisation was known or likely to occur. Findings in relation to the distribution, structure and impacts of the mussel masses themselves, and on the composition of the associated biota within these masses, are discussed below.

Distribution and abundance of infected kelp plants

M. galloprovincialis are almost exclusively intertidal in their distribution and generally do not occur in the subtidal zone. The reasons for this are not understood, as the species settles and grows well on mussel culture ropes that hang 8 m or more into the subtidal zone (Branch and Steffani 2004). It is possible that settling in the subtidal zone makes the mussels more vulnerable to predation and that the kelp beds provide a protected habitat for them in this zone. Within the kelp bed, *M. galloprovincialis* were absent from kelps growing in water shallower than 2 m and significantly more likely to be found on kelp heads in the outer edge of the kelp bed, in water deeper than 5 m ($p < 0.001$). As mussels filter fine food particles from the water, this is likely due to the increased water movement and food abundance found towards the outer boundary of the kelp beds (Dial and Roughgarden 1998).

Infected kelp stipes were found to be very rare, with only two recorded amongst 735 kelps examined in the transects, while infected heads were much more common, with 74 found among the kelp surveyed. Possibly the greater frequency of mussels on the kelp heads is because these are buoyant and essentially occur in the intertidal zone, the preferred habitat of this species of mussel (Branch and Steffani, 2004). Alternatively, this could be because the kelp heads provide a complex 3-dimensional habitat with more opportunities for attachment than the smooth, slippery stipes. No relationship could be investigated between the infection rate of kelp

stipes and depth due to the extremely low sample size of two. Additional sampling effort would be required to further investigate this relationship.

Relationship between mussel mass and stipe length

No significant relationship was found between stipe length and the biomass of mussels on the heads of the kelps, although there was a larger amount of variation on kelps with longer stipes (Figure 4). The lack of relationship could be due to the small sample size, plus high variability within the mussel masses.

There was no significant relationship found between mussel mass and stipe length on infected kelp stipes. Again the lack of relationship could be due to the high degree of variability within the mass of mussels growing on stipe samples. An increase in the sample sizes would allow for further investigation of this relationship.

Position and composition of mussel masses

Sections of kelp stipe between 150 cm and 250 cm above the seafloor were more likely to be infected with mussel masses, with the data displaying a normal distribution (Figure 6). The reasons for this could be that mussels that settle too close to the substratum are still accessible to the predators that are presumed to prevent them surviving in benthic habitats. Those too high on the stipes could also be subject to increased wave action and turbulence and this may prevent them being able to grip the flexing stipe during storms. Due to the small sample size of infected stipes, additional sampling is required to further investigate this relationship

Mostly small mussels (almost all < 60 mm shell length) were found on kelps in this study, which could indicate that this colonisation of kelps has only began in the past few years. This is in line with anecdotal evidence that mussels were not observed growing on kelp plants in False Bay until 2016 (Foster C, *pers. comm.*). In Saldanha Bay on the Atlantic seaboard of the Western Cape, *M. galloprovincialis* were shown to grow on average 33 mm per year (van Erkom Schurink and Griffiths 1993). The current study found very few mussels above 60 mm and none above 90 mm, indicating the mussels found are less than three years old. *M. galloprovincialis* also grow quicker in warmer water, so the growth rate in False Bay may be even higher than in Saldanha Bay, meaning the mussels in False Bay could be even younger than indicated (van Erkom Schurink and Griffiths 1993).

The infection rate of heads was much higher than that of stipes however the largest mussel mass was found on a stipe sample and stipe samples had much larger mussel masses, with a median of 595.5 g (194.0 to 955.0 g) compared to 86.4 g (14.8 to 353.8 g) on heads. This could be due to the submerged nature of stipes creating a more protected habitat once colonisation has been established, or simply because stipes provide a larger surface area for settlement than heads because they are longer.

M. galloprovincialis also have the potential for extremely high levels of recruitment of up to 20,000 recruits per m^2 (Harris et al. 1998), so it is possible that the infestation of kelps could have been the result of one or more extremely successful breeding years. Further study is needed to determine if this invasion on kelp in False Bay will continue in future years.

Buoyancy

M. galloprovincialis are negatively buoyant in sea water (their mass when submerged being approximately 33% of their mass in air). Measurements of the weight of mussel masses while submerged in seawater showed that they can considerably reduce the buoyancy of the kelp to which they are attached and, in extreme cases, this can result in toppling over and sinking of the kelp heads, which was observed during field work (Figure 2C). However, the mussel masses recorded had the potential to cause negative buoyancy in less than 20% of kelp plants measured in this study, with stipe samples having a higher median mussel mass. Fortunately mussel masses on stipes are very rare, so this phenomenon is unlikely to have a significant impact on the kelp bed as a whole. Mussel masses on kelp heads are, however, common (occurring on 10% of kelps examined during transects at all four sites) and thus have the potential to topple many more kelp plants. The added mass of mussels on the kelp heads possibly also creates more leverage for the mussels to topple the plant. Starfish have then been observed eating the mussels once the kelp topples over (Foster C, *pers. comm.*) and further study could investigate if these kelp will then regain positive buoyancy if starfish eat many or all of the mussels. As this colonisation has likely recently begun, further study is needed to determine if larger mussels will begin growing on kelp plants, further reducing their buoyancy and increasing the mortality rate of kelp plants in False Bay. Additionally, more sites around False Bay will need to be investigated as this study only targeted four sites where infection was known or likely to occur.

Fauna and flora associated with mussel masses

Stipe samples had a much higher number of species overall (86) than head samples (41). This is partly due to stipes having larger mussel masses (approximately triple on average) than heads. However, stipe samples consistently support more species than head samples of similar mass (Figure 9). The reason larger mussel masses support more species is likely due to their increasing surface area and increasing complexity and volume of protected habitat (Robinson et al. 2007; Sadchatheeswaran et al. 2015). The reason stipe samples had more species than head samples with mussel masses of the same size could be due to the fact that stipes are the continuously submerged and that they are subject to less turbulence than heads.

Mollusca, Polychaeta and Crustacea were common on both head and stipe samples, indicating that overall the groups do not have a strong habitat preference between heads and stipes. Echinodermata showed a strong preference for stipe samples with five times the number of species found on stipe samples than head samples. Bryozoa also had a strong preference for stipe samples, with over four times the number of species than found on head samples. A larger biomass of green (Chlorophyta), brown (Ochrophyta) and red algae (Rhodophyta) and of Ascidiacea were also found on stipe samples, indicating a preference for the more protected submerged habitat. The only group that showed a strong preference for infected kelp heads was Hydrozoa. The current study also found one un-described species of Amphipod discovered on head species during this study (Figure 12), however, as this species burrows into the tissue of the kelp heads, its presence is unlikely to be related to the presence of mussel masses.

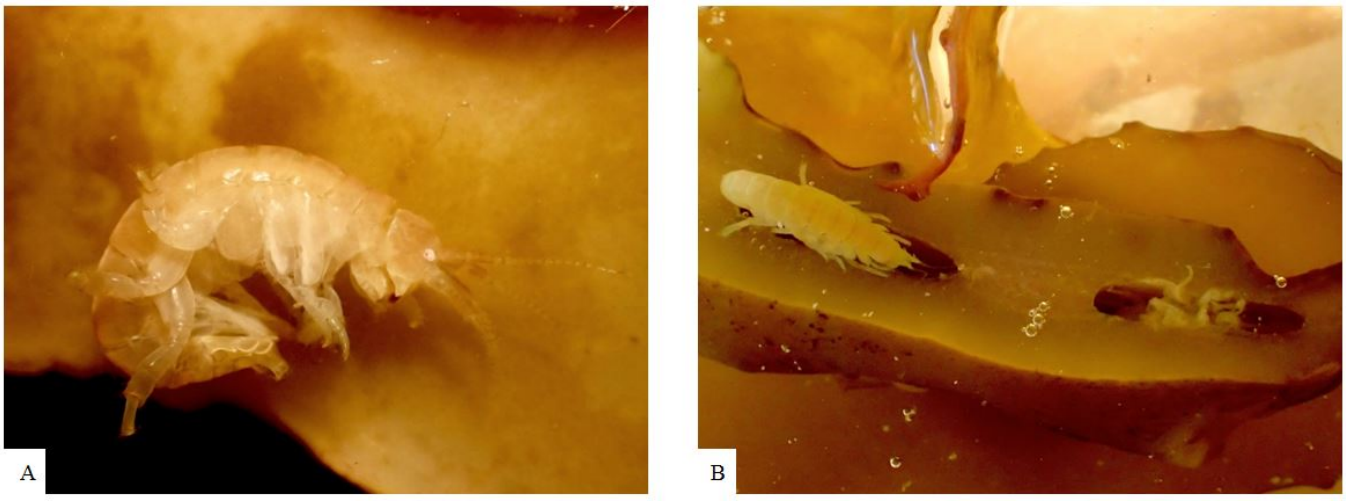

Figure 12. A) New species of amphipod *Peramphithoe n. sp.* **B)** amphipod burrowing into kelp head (photos: Charles Griffiths).

Six species known to be alien to the Western Cape, the *M. galloprovincialis* (invasive), three Bryozoans; *Watersipora subtorquat*a (invasive), *Viridid*e*ntula dentata* and *Bugula sp*., an Amphipod *Melita oba* and the Hydrozoa *Obelia dichotoma*, were found living in the mussel masses. The mussel masses may create a protected environment (Robinson et al. 2007) which aids their survival during long-distance kelp rafting events. Jarman and Carter (1981) estimated that about 12% of kelp is removed by storms annually, but mussel masses will increase the drag on kelps and may raise the mortality rate. The buoyancy reduction from the mussels was generally not enough to sink infected kelp plants if they are dislodged, therefore, the infected kelp plants have the potential to raft vast distances. Holdfasts were found to have a minimal negative effect on buoyancy (-39 g on average), and so whether or not they remain attached to the kelps would make little difference to buoyancy and rafting. Although many kelp plants will be washed ashore immediately, there is the potential for kelp to raft 1000s of kilometres (Arnaud et al. 1976). However the mussels will continue to grow after the plants detach, which could limit travel distances if the mussels become large enough to sink the kelp. Therefore the rafting events have the potential to spread not only known alien species, but also native South African species to areas where they may become invasive.

Diversity in head samples appeared to reach the asymptote, indicating that no more samples needed to be collected to adequately sample biodiversity in this habitat, but stipe samples would require additional sampling to reach the asymptote. It is likely that species richness will keep increasing if more stipe samples are collected. The stipe samples overall had a higher Shannon's Diversity index and species richness than head samples, however significant differences were not found in the Shannon Diversity indices of head and stipe samples.

The sample ordination illustrated the dissimilarity (in terms of species composition) between infected head and stipe samples. Although there were some groupings of head samples and some of stipe samples there were many species that overlapped. There was however a significant difference in the biota found on head and stipe samples ($p = 0.018$). Species found on heads were likely different than those found on stipes because the environment on kelp heads requires them to tolerate spending part of their time out of the water and to survive increased turbulence from breaking waves on the surface.

Community composition

The total number of species found on both heads and stipes in this study was 94, compared to only 23 found by Allen and Griffiths (1981) in their study of the epiphyte composition of *E. maxima* at Oudekraal on the west coast of the Cape Peninsula (Figure 13).

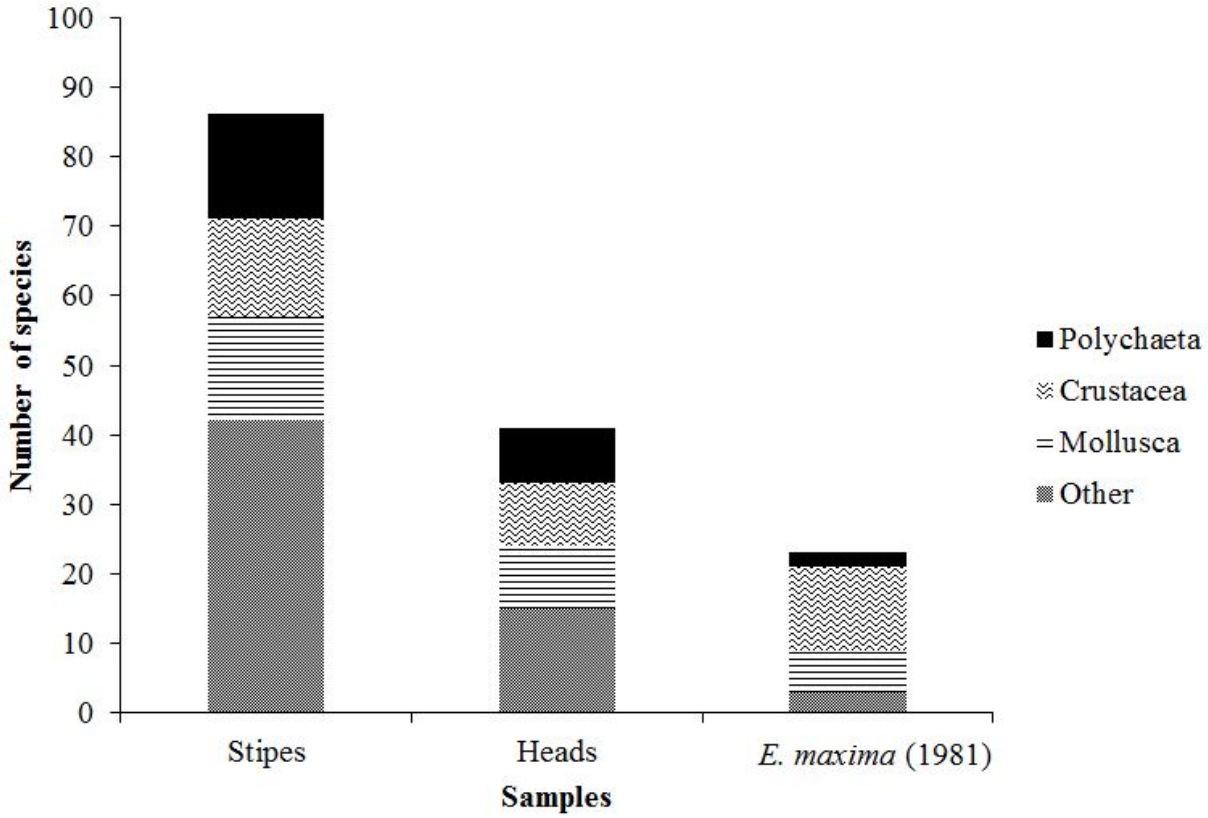

Figure 13. Biological community composition of stipe samples, head samples and epiphytes of the kelp *E. maxima* (Allen and Griffiths, 1981). 'Other' is Porifera, Actiniaria, Hydrozoa, Platyhelminthes, Nemertea, Bryozoa, Echinodermata, Ascidiacea and algae (Rhodophyta, Chlorophyta and Ochrophyta).

The increase in the number of species found in the present study may be due to the extra substrate created by the mussels, providing a more protected habitat for other organisms to live on. This comparison must be treated with some caution though, since False Bay and Oudekraal lie in different biogeographic zones. Oudekraal, where the previous study was undertaken, although geographically close to the present study site, is located in the Benguela Marine Province, which extends from Cape Point northwards into Namibia and is characterised by cooler water temperatures than the Agulhas Marine Province, which extends from Cape Point to the Eastern Cape (Smit et al. 2013). Understory kelp bed communities differ between False Bay and the west coast (Anderson et al. 1997; Leliaert et al. 2000) and differences might also be

expected among communities epiphytic on kelp plants. In addition, different sampling techniques were used between the two studies so certain mobile taxa, such as small Crustacea, were less likely to be captured in the current study than in that of Allen and Griffiths (1981) which brought kelps ashore inside a fine net.

There are notable differences in composition of the fauna between the two studies. The samples of Allen and Griffiths (1981) were dominated by Crustacea (12 species), while the present study found the 'other' category (e.g. Hydrozoa, Bryozoa, algae and Ascidiacea) had the most species on both infected kelp heads and stipes. Indeed, there were only seven species common to both the present study and that of Allen and Griffiths (1981) which could be due to the presence of mussel masses on the False Bay kelp plants. Interestingly, the black mussel (*Choromytilus meridionalis*) recorded by Allen and Griffiths (1981) is likely a misidentification of *M. galloprovincialis* (Griffiths CL, *pers. comm.*). *M. galloprovincialis* was just starting to colonise the area in 1981 (Griffiths et al. 1992), but was not officially described until 1985 (Grant and Cherry 1985). Due to the fact that it is now the most common mussel in the area, that juveniles of the two species are difficult to distinguish, and no black mussels were found during the course of the current study, it seems very likely that the mussel identified in 1981 was the *M. galloprovincialis*.

The main limitations of the present study were the small samples sizes due to the short timeframe allowed to complete the experimental study, leading to a lower statistical power. Additionally, not enough infected stipe samples were found to reach the asymptote of the species accumulation curve. This study also targeted kelp beds that were known or likely to have mussel infections so the distribution and abundance of mussel masses found in our investigation may be higher than what is occurring in the rest of False Bay.

Conclusion

During the course of this study in False Bay, it was found that *M. galloprovincialis* were more likely to occur on kelps towards the outer edge of kelp beds where there is more water movement, and mussel masses are much more frequently found on kelp heads than on stipes. In addition, mussels infecting the kelp beds were likely younger than three years, indicating that colonisation has only recently begun. While the buoyancy of kelp plants was reduced by the invasion of mussels, it was not enough to sink most kelp plants. Lastly, the mussel masses

increased the species richness of the biota epiphytic on kelps, on both infected heads and stipes, and six known alien species (two invasive) to the Western Cape were found on infected kelp plants. Because detached kelp can raft vast distances, there is the potential for mussel infected kelps to spread not only alien species, but also native South African species, to locations where they could become invasive. Further investigation is required on this novel phenomenon, especially to determine if the infection rate of kelp forests in False Bay is increasing or spreading to other locations.

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